
WINTERACEAE EVOLUTION: AN ECOPHYSIOLOGICAL PERSPECTIVE¹

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ABSTRACT

The Winteraceae have long been regarded as the most primitive living family of angiosperms. The justification for this view partly arises from their lack of xylem vessels. Because xylem vessels have been considered a key innovation in allowing angiosperms to rise to their current ecological dominance, Winteraceae have been portrayed as declining relicts, limited to wet forest habitats where their tracheid-based wood does not impose significant hydraulic constraints. However, phylogenetic analyses indicate that the vesselless wood of Winteraceae may be secondarily derived, while extension of the Winteraceae fossil record into the Early Cretaceous suggests that this family has a more complex ecological history than can be deduced from their current distribution. These observations motivate a re-examination of the functional significance and selective pressures underlying the pattern and direction of character change of the distinctive features of this family. In particular, physiological studies on stomatal plugs and xylem hydraulic parameters are consistent with their ecological success in wet, temperate environments.

Key words: stem water transport, tracheids, *Takhtajania*, Winteraceae, xylem evolution.

The first angiosperms have been traditionally portrayed as slow-growing trees characterized by “primitive” morphological features and confined to wet tropical environments (Bailey, 1944; Takhtajan, 1969; Carlquist, 1975; Cronquist, 1981). According to this woody-tree hypothesis, Winteraceae are the least modified descendants of this hypothetical angiosperm ancestor (van Tieghem, 1900; Thompson & Bailey, 1916; Bailey & Thompson, 1918; Bailey, 1944; Smith, 1945; Takhtajan, 1969; Thorne, 1974). A major reason for this association is the absence of xylem vessels in Winteraceae (van Tieghem, 1900; Bailey & Thompson, 1918; Bailey, 1944; Cronquist, 1981; Carlquist, 1983, 1987, 1996; Gifford & Foster, 1989), although the presence of other putatively primitive morphological characters has been used to reinforce this view (Bailey & Swamy, 1951; Thorne, 1974; Hickey & Wolfe, 1975). A logical extension of this perspective is to view Winteraceae as an evolutionary dead end, confined to wet forest refugia where primitive aspects of their morphology and ecology would not be disadvantageous (Bailey, 1944, 1953; Bailey & Nast, 1945; Smith, 1945; Takhtajan, 1969; Carlquist, 1975, 1983). In particular, Winteraceae have been described as limited to understory habits well

suited to their presumably inefficient xylem, with their survival further enabled by the evolution of a distinctive leaf-level feature, i.e., waxy plugged stomata (Bailey, 1944, 1953; Bailey & Nast, 1944; Baranova, 1972; Carlquist, 1975, 1996; Cronquist, 1981).

Recent findings on the phylogeny of angiosperms and the paleoecology and physiological ecology of Winteraceae challenge the idea that Winteraceae represent an unchanged lineage (Young, 1981; Donoghue & Doyle, 1989; Doyle et al., 1990; Chase et al., 1993; Crane et al., 1995; Soltis et al., 1997; Nandi et al., 1998; Feild et al., 1998; Doyle, 1998, 2000; Mathews & Donoghue, 1999). Our goal in this paper is to review Winteraceae’s ecological characteristics in relationship to historical changes in their distribution and climatic associations. In particular, we focus on how physiological studies, combined with paleoecological and biogeographic information, alter our perspective on two of the most distinctive features of Winteraceae: stomatal plugs and vesselless wood. The impact of the re-discovery of *Takhtajania perrieri* (Capuron) Baranova & J.-F. Leroy (Schatz et al., 1998) on our understanding of the ecological evolution of the Winteraceae will also be considered.

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Table 1. Classification and geographic distribution of modern Winteraceae. Nomenclature and distributions follow Smith (1942, 1943a, b). Ecological distributions were compiled from Feild (unpublished obs. in Australia, Costa Rica, New Caledonia, and New Zealand), G. Schatz (pers. comm. 1998), Smith (1942, 1943a, b), and Vink (1970, 1977, 1985).

Genus	Distribution	Ecology
<i>Belliolum</i> (6–7 species)	New Caledonia, Solomon Islands	Understory and subcanopy treelets to trees in subtropical lowland rainforest
<i>Bubbia</i> (?33 species)	Australia, Lord Howe Island, New Caledonia, New Guinea, Solomon Islands	Shrubs, treelets, to large trees (15 m+) in tropical premontane, montane cloud forest; in New Caledonia some species on serpentine soils
<i>Drimys</i> (6 species)	Central America, Mexico, South America	Subcanopy and canopy shrubs to trees in tropical montane cloud forest, maritime temperate rainforest, páramos
<i>Exospermum</i> (2 species)	New Caledonia	Large trees in subtropical lowland rainforest
<i>Pseudowintera</i> (2 species)	New Zealand	Subcanopy trees, alpine shrubs
<i>Takhtajania</i> (1 species)	Madagascar	Treelets to subcanopy trees in montane cloud forest (~1000 m)
<i>Tasmania</i> (5–30+ species)	Australia, Borneo, Indonesia, Philippines, New Guinea	Diverse growth forms in alpine and lowland temperate rainforests, tropical lowland forest, tropical montane cloud forest
<i>Zygogynum</i> (6 species)	New Caledonia	Subcanopy trees in subtropical lowland rainforest and montane cloud forest

ECOLOGICAL CHARACTERISTICS OF LIVING WINTERACEAE

Winteraceae, with 65 species in four to six genera (Smith, 1942, 1943a, b; Vink, 1988; Suh et al., 1993), are a diverse evergreen assemblage with growth forms that include minute-leaved epiphytes, terrestrial alpine shrubs and scramblers, large-leaved understory treelets, and medium-sized (~20 m tall) trees (Smith, 1942). Although generally limited to wet habitats (rainfall > 1200 mm/year), they can be found in a variety of habitats ranging from subtropical montane mossy rainforests to cool coastal and montane temperate rainforests, and subalpine and alpine shrubberies. *Tasmania lanceolata* (Poir.) A. C. Smith is an exception that occurs as a small tree in moist sites such as gullies and stream margins in dry sclerophyll-dominated woodlands (rainfall about 800 mm/year) in Tasmania. The current distribution of Winteraceae follows a southern Gondwanan geographic pattern with most species and genera in Australasia (Table 1; Raven & Axelrod, 1974; Schuster, 1976; Raven, 1980), excepting *Drimys granadensis* L. and *Tasmania piperita* Hook., which currently extend into regions outside of Gondwana. *Drimys* is the sole genus represented in the New World, where it occurs from cold, wet Magellanic rainforests in southern Chile and Argentina to the tropical and temperate highlands of Mexico (Veblen et al., 1995). Finally, the monospecific genus *Takhtajania* is

found only in cool montane forests of northeastern Madagascar (Schatz et al., 1998).

Winteraceae are most diverse in subtropical regions (Vink, 1970, 1977, 1985, 1993), but ecologically more successful in terms of their abundance in temperate environments. Within the subtropics, Winteraceae are found in areas with abundant precipitation and/or low evaporative demand such as along rivers, in understory habitats, and in everwet mossy montane forests (Smith, 1942, 1943b; Vink, 1970, 1977, 1985, 1993; Jaffré, 1995). Populations of many Winteraceae such as most *Bubbia* and *Zygogynum* species in the subtropics consist of only a few individuals (Smith, 1942; Vink, 1977; Pellmyr et al., 1990). A potential contributing factor to this low density may be the tendency for limited seed production due, in part, to infrequent pollinator visits (*Sabatinca* moths, *Palontus* weevils; Pellmyr et al., 1990). Most species of subtropical Winteraceae are tolerant to shade and occur as understory treelets (1–4 m tall) and infrequently as subcanopy trees (to 10 m tall) that become established late during succession (Vink, 1993; T. S. Feild, unpublished obs.). Many of these treelets have exceptionally large leaves (15–30 cm in length is not uncommon especially in *Belliolum*) compared to other Winteraceae from cooler climates, which cause plants to appear “top heavy” and susceptible to breakage (Vink, 1970, 1993; T. S. Feild, unpublished obs.). Another characteristic

of some Winteraceae is their ability to reproduce vegetatively by stem sprouting. *Tasmannia piperita* in New Guinea is reported to reproduce primarily by stem sprouts, while other subspecies are known to reproduce by subterranean stolons (Smith, 1943b; Vink, 1970). Profuse stem sprouting, resulting in multiple-branched plants, occurs in *Bubbia*, *Drimys*, *Pseudowintera*, *Takhtajania*, and most species of *Tasmannia* (Vink, 1970; Raleigh et al., 1994; T. Feild, unpublished obs.; G. Schatz, pers. comm. 1998).

The view of Winteraceae as an ecologically restricted group is difficult to reconcile with its high abundance in wet, temperate rainforest habitats (ca. 3000 mm a year, with frequent frost and some snow). In temperate areas, Winteraceae species can dominate the understory and subcanopy as well as grow in exposed habitats. For example, *Drimys winteri* forms dense subcanopy thickets in coastal Chilean temperate rainforests and occurs frequently as a large canopy tree, 19 m tall and up to 65 cm trunk diameter (Lusk, 1993). Winteraceae are also abundant as individuals in subalpine and alpine communities of Australia, Chile, New Guinea, and New Zealand, where freezing can occur at any time of the year (Vink, 1970; Barry, 1980; Kirkpatrick, 1983, 1997; Veblen et al., 1995). All four major clades within Winteraceae (*Bubbia*, *Drimys*, *Pseudowintera*, and *Tasmannia*, as inferred from molecular phylogenetic analyses using ITS rDNA; Suh et al., 1993) contain species that grow as small-leaved (< 1–3 cm long) shrubs and small trees in high-altitude wet montane communities (Smith, 1943a; Hope, 1980; Nunez et al., 1996). In Tasmania, *Tasmannia lanceolata* occurs as an abundant prostrate shrub (e.g., approx. 45% cover) on rocky scree slopes well above the eucalypt and *Nothofagus* tree lines, where it is found alongside conifers such as *Diselma* (Cupressaceae) and *Microstrobos* (Podocarpaceae) (Gibson et al., 1995; Kirkpatrick & Bridle, 1999). *Drimys granadensis* grows as a multiple-branched shrub in *Espeletia*- (Asteraceae) dominated wet páramos of Colombia (Smith, 1943a). In New Zealand, *Pseudowintera colorata* and *P. traversii* grow in the company of conifers on alpine plateaus and mountain tops, where they are gregarious colonizers of landslides (Stewart & Harrison, 1987).

Within these temperate habitats, Winteraceae appear to be good competitors. Rebertus and Veblen (1993) reported that *Drimys winteri* produced a substantial rain of viable seeds, and seedlings grew rapidly in response to forest gap formation, impeding the recruitment and growth of *Nothofagus* (Nothofagaceae) and other vessel-bearing angiosperms. *Drimys* apparently requires large-scale dis-

turbances, such as large gaps produced by wind damage and multiple treefalls, to become established (Rebertus & Veblen, 1993). However, with distance from the coast, *Drimys* abundance decreases rapidly, perhaps reflecting a reduction in water availability (Rebertus & Veblen, 1993). Early succession recruitment of Winteraceae occurs in other temperate taxa. *Tasmannia lanceolata* is an abundant colonizer of open fields on the central basalt plateau of Tasmania, which has frequent frost in the winter (Read & Hill, 1983). This species forms dense thickets in grasslands, understories of dry sclerophyll woodlands (~ 800 mm rainfall a year), and on slopes of wet eucalypt gullies (Vink, 1970; Raleigh et al., 1994). *Tasmannia piperita* dominates forest edges in subalpine rainforests and penetrates into frost-stricken grasslands of high altitudes (> 3000 m) in New Guinea (Vink, 1970; Hope, 1980). *Tasmannia piperita* is also common on landslide-exposed soils in montane habitats (Hope, 1980).

PALEOECOLOGICAL AND PALEO GEOGRAPHIC HISTORY OF WINTERACEAE

To understand Winteraceae's ecological success (in terms of abundance of individual plants) in wet temperate versus subtropical environments, historical patterns of Winteraceae distribution, continental movements, and climatic changes must be considered. The extensive recovery of Winteraceae fossil pollen (tetrads) indicates that Tertiary and Late Cretaceous Winteraceae shared a similar Southern Hemisphere temperate distribution with modern Winteraceae (Coetzee & Muller, 1984; Coetzee & Pragowski, 1988; Dettmann & Jarzen, 1990; Doyle et al., 1990; Dettmann, 1994; Macphail et al., 1994; Doyle, 2000). The oldest Australasian pollen (collected in southeastern Australia) is from the Campanian (Dettmann & Jarzen, 1990), indicating that, at 80 Ma BP, the geographic range of Winteraceae corresponded to the Southern Gondwana flora province of Brenner (1976). This region was a moist, cool temperate region dominated by conifers (Podocarpaceae, Araucariaceae) and later included the austral angiosperms *Nothofagus* and Proteaceae (Axelrod, 1984; Dettmann & Jarzen, 1991; Spicer et al., 1993; Srivastava, 1994; Hill & Scriven, 1995). Specht et al. (1992) suggested that during the Late Cretaceous, Winteraceae, along with Trimeniaceae, *Ilex* (Aquifoliaceae), and Proteaceae, were understory shrubs growing in temperate lowland forests (mean annual temperature ~ 12°C) dominated by podocarps and proteaceous trees (e.g., *Knightia*, *Macadamia*). These for-

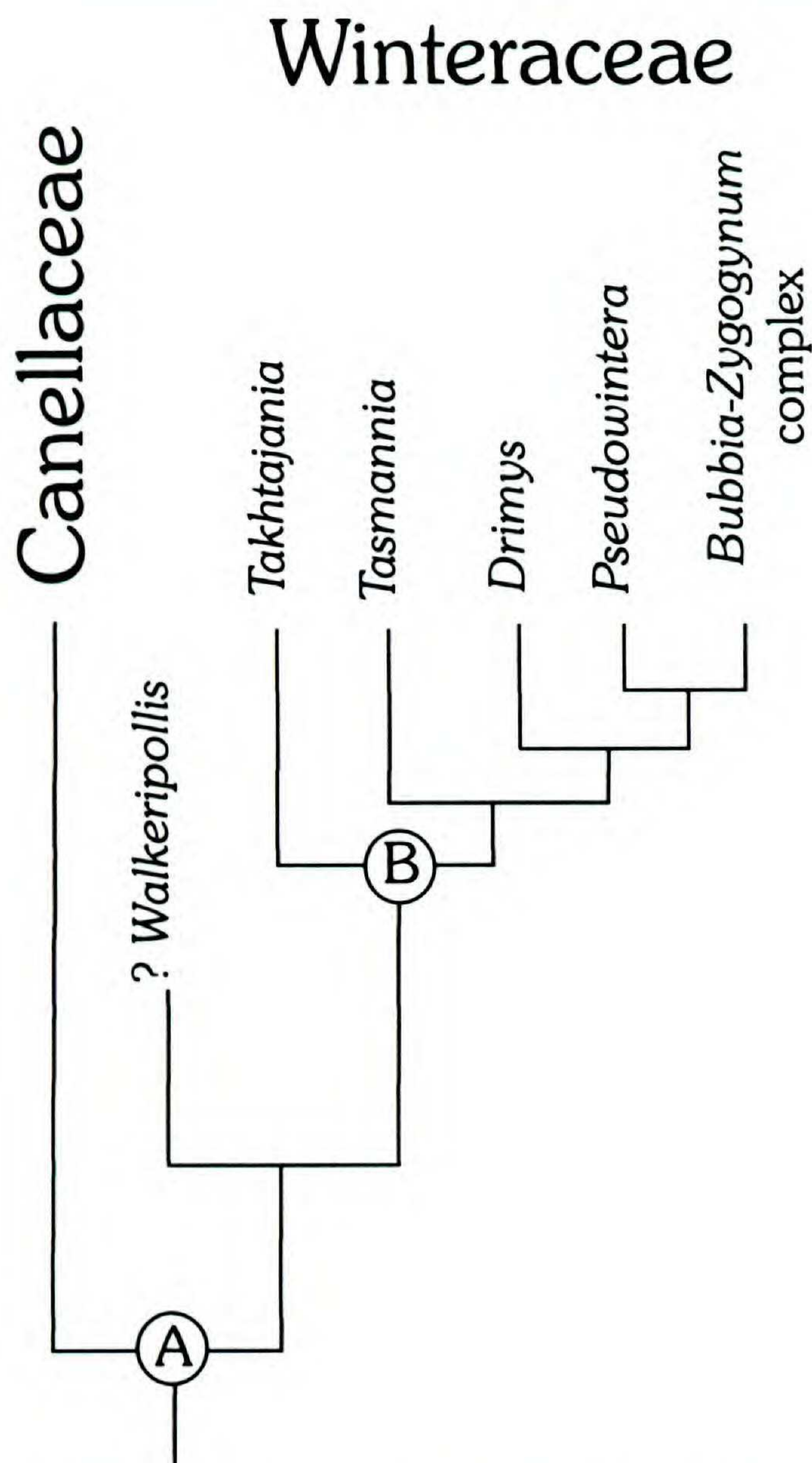


Figure 1. Phylogenetic hypothesis for the relationships among Winteraceae, based on the molecular phylogeny of Suh et al. (1993), the fossil pollen genus *Walkeripollis* (Doyle et al., 1990), and Canellaceae (Chase et al., 1993). Node A is the split from Canellaceae, while node B represents the lineage that gave rise to all extant Winteraceae as well as Late Cretaceous and Tertiary fossil pollen taxa distributed in Australasia (Doyle et al., 1990). *Walkeripollis* may represent an extinct side-branch, found in Northern Gondwana, that pre-dates the origin of node B (Doyle et al., 1990).

est associations occurred in what is now southern Australia and Antarctica; however, no modern analog of this forest community exists today (Specht et al., 1992; Dettmann, 1994; Hill & Scriven, 1995).

Understanding of the climatic and geographic distribution of Winteraceae was greatly enhanced by the discovery of considerably older winteraceous pollen (Late Barremian–Early Albian, 125–105 Ma BP) in several localities well to the north of Southern Gondwana (e.g., Israel and Gabon (Walker et al., 1983; Doyle et al., 1990; Brenner, 1996)). Cladistic studies of these fossils indicate that the

plants that produced them were more primitive than the common ancestor of Late Cretaceous, Tertiary, and modern genera of Winteraceae (Fig. 1; Doyle et al., 1990). Surprisingly, these putatively related tetrads occurred within the Cretaceous subarid tropical belt of northern Gondwana (Doyle et al., 1990; Srivastava, 1994; Brenner, 1996; Doyle, 2000). A major implication of these fossils is that the Late Cretaceous Winteraceae and their extant descendents are a temperate branch from an initially tropical lineage that spread southward from Northern Gondwana (Fig. 1; Doyle et al., 1990). Thus, the Australasian regions that include the current center of Winteraceae diversity, such as New Caledonia, (Vink, 1993), are not the cradle of Winteraceae evolution (Dettmann & Jarzen, 1990; Doyle et al., 1990; Dettmann, 1994).

A Northern Gondwanan origin suggests that early Winteraceae were likely to have experienced substantial changes in climate during their migration into the Southern Hemisphere. Two migratory routes into Australasia appear plausible, based on known distributions of fossil winteraceous pollen (Fig. 2; see Doyle, 2000, for more discussion). In the first of these scenarios, Winteraceae reached Australasia through an overland dispersal corridor that included temperate South America and Antarctica (Raven, 1980). An alternative scenario is that the wet temperate Winteraceae lineage originated and radiated in Africa during the Middle Cretaceous (Coetzee & Pragowski, 1988) before dispersing first to Madagascar, and then via over-water dispersal into temperate Australia with Antarctica providing an overland route (Fig. 2B). Presently, it is not clear which of these scenarios is more probable because of the large temporal gap (~ 25 Ma) in fossil pollen data between the first appearance of winteraceous pollen in northern Gondwana and the occurrence of fossils resembling modern Winteraceae in southern Australia (Doyle et al., 1990; Dettmann, 1994; Macphail et al., 1994; Doyle, 2000). Local extinction of Winteraceae, implied by fossil pollen in Africa and central Australia, makes interpretation of their biogeography especially problematic (Coetzee & Muller, 1984; Macphail et al., 1994). Regardless of the route taken to reach Australasia, the fossil pollen record indicates that extant Winteraceae were derived from an originally tropical lineage that migrated into relatively cold areas. This suggests that distinctive features of this family might be associated with success in wet temperate environments.

STOMATAL PLUGS: KEEPING WATER IN OR OUT?

Despite the occurrence of most Winteraceae in wet environments, their leaves possess several

A. South American Origin

B. African Origin

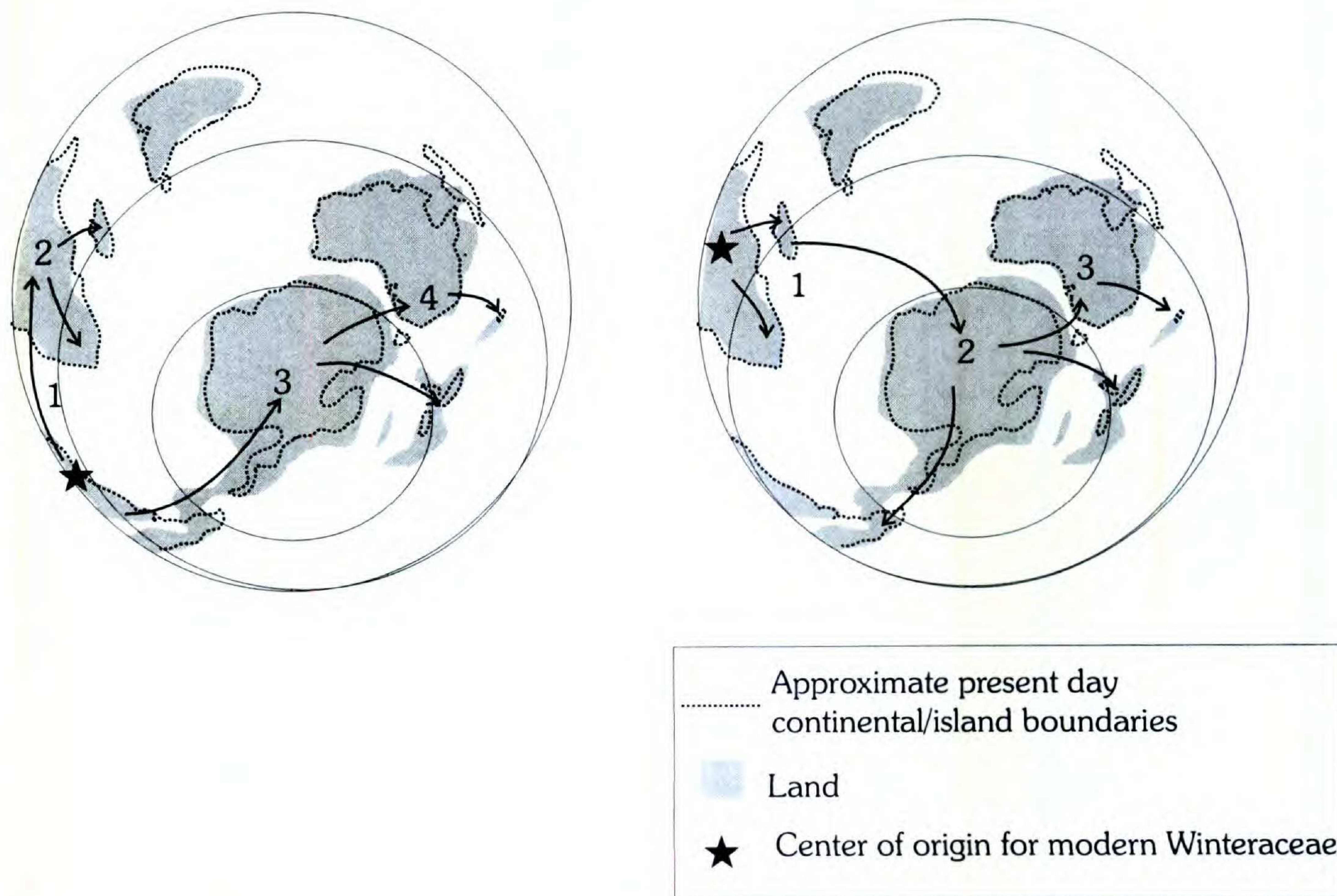


Figure 2. Two paleogeographic hypotheses for the center of origin and routes of migration of Winteraceae into Australasia. The arrangement of continental areas is from the Late Cretaceous (Early Campanian, 80 Ma BP) when fossil pollen closely resembling modern “crown-group” Winteraceae first appeared (Dettmann & Jarzen, 1990). —A. In the first route, Winteraceae originated in temperate regions of southern South America following dispersal from Northern Gondwana (1). To account for Winteraceae pollen in Africa and *Takhtajania* in Madagascar, dispersal to Africa and then Madagascar must be invoked (2). Winteraceae would then have moved across Antarctica into Australasia (3 and 4). —B. An alternative route may have involved the origination of temperate Winteraceae in Africa (possibly southern areas) with *Takhtajania* as a surviving descendant from this radiation. Winteraceae may have then dispersed overwater or possibly overland into Antarctica (1) and finally into other Australasian regions (2 and 3). Stars indicate the centers of origin for node B Winteraceae (see Fig. 1).

seemingly xeromorphic features. To varying degrees, Winteraceae leaves have thick cuticles and/or the stomata are sunken into the abaxial leaf surface (Bailey & Nast, 1944; Baranova, 1972; Bongers, 1973). Perhaps the most striking manifestation of Winteraceae’s apparent xeromorphy is the obstruction of each stomatal pore with a granular “plug” composed of cutin and wax (Fig. 3; Bailey & Nast, 1944; Baranova, 1972; Bongers, 1973; Feild et al., 1998). These structures are responsible for the characteristic white reflective appearance of the undersurfaces of Winteraceae leaves (Bailey & Nast, 1944).

The diversity of stomatal ornamentation found in Winteraceae is enormous (Bongers, 1973). In *Takhtajania* and some species of *Tasmannia*, stomatal plugs are absent (Fig. 3A; Baranova, 1972; Bon-

gers, 1973). In others (most *Tasmannia* species), the stomata are only partially occluded by the presence of small crystalline wax rodlets confined to the guard cell rims (Vink, 1970; Bongers, 1973). The abaxial epidermal surfaces of *Drimys brasiliensis* Miers and some entities of *Tasmannia piperita* are covered with dense overarching papillae formed from extensions of the cuticular layer (Smith, 1943a; Bailey & Nast, 1944; Bongers, 1973). Finally, in some *Bubbia* and *Zygogynum* species, the stomatal apparatus is completely buried under a mat of encrusting wax rodlets and an additional layer of cuticle such that the stomata cannot be seen (Bongers, 1973; Metcalfe, 1987; Vink, 1993).

A long-held belief has been that stomatal plugs and the other apparently xeromorphic leaf features of Winteraceae function to restrict water loss (Bai-

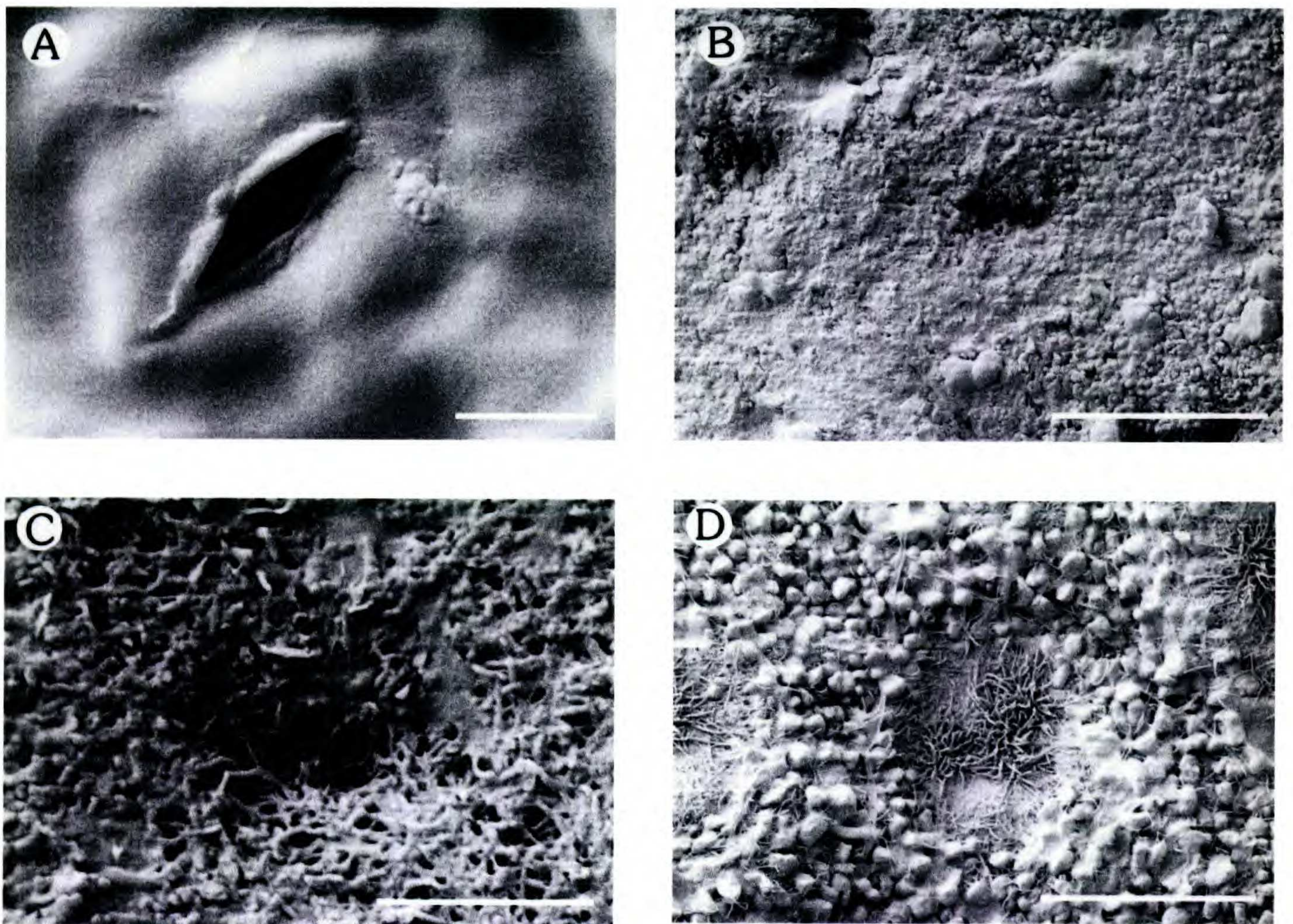


Figure 3. Diversity of stomatal ornamentation in Winteraceae. —A. A stoma of *Takhtajania perrieri*, which is completely free of waxy obstruction. —B. Epidermal surface of *Drimys granadensis*, which is covered with pieces of cuticle and granular waxes. The stomata, which are indicated by the dark clefts, reside below the epidermal layer. —C. Close-up of porous crystalline rodlets associated with a stoma of *Pseudowintera axillaris* (J. R. & G. Forst.) Dandy. —D. *Belliolum rivularis* (Parmentier) Burt epidermis, which has a dense mat of cuticular papillae (visible between the stomatal regions) and a concentration of tubes (possibly composed of wax or cutin associated specifically with the stomatal apparatus). Scale bars are: 5 μm (A & C) and 20 μm (B & D).

ley, 1944, 1953; Bailey & Nast, 1944; Baranova, 1972; Carlquist, 1975; Cronquist, 1981). As anti-transpirants, these structures were proposed to have evolved to compensate for the presumed inferiority of a tracheid-based transport system (see below; Bailey, 1944, 1953; Bailey & Nast, 1944; Baranova, 1972; Carlquist, 1975; Cronquist, 1981; Sperry, 1995). Stomatal plugs also occur in most Southern Hemisphere conifers, such as Araucariaceae, Cupressaceae, Podocarpaceae, as well as many northern groups, which has fueled discussions on a functional linkage between stomatal plugs and the absence of xylem vessels (Jeffree et al., 1972; Yoshie & Sakai, 1985; Wells & Hill, 1989; Stockey et al., 1992; Carlquist, 1996; Stockey & Atkinson, 1993; Stockey & Frevel, 1997; Brodribb & Hill, 1998; Stockey et al., 1998).

The hydraulic compensation argument has been applied to Winteraceae for many years, despite the absence of any information on how stomatal plugs affect rates of leaf gas exchange. In contrast to what

their name suggests, stomatal plugs are not solid, but riddled with air-filled pores formed between tubes of cutin and granular wax crystals (Bongers, 1973). Although a porous construction is necessary for CO_2 uptake, this fact seems to have been overlooked in arguments of presumed transpiration-retarding effects. Recently, Feild et al. (1998) examined how these structures influence water loss rates from *Drimys winteri* var. *chilensis* (DC.) A. Gray leaves. Comparisons of plugged and “unplugged” leaves (leaves from which stomatal plugs and associated epicuticular waxes were experimentally removed) demonstrated that under high relative humidity (85%) plugs posed a relatively small resistance to leaf water loss (Feild et al., 1998). Maximum stomatal conductances of *Drimys* leaves with stomatal plugs were about 10% lower than leaves from which the stomatal plugs had been experimentally removed. Maximum conductances of plugged leaves (approx. $100 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), although lower than many lowland rainforest trees

and crop plants, were similar to those reported from other montane cloud forest angiosperms (Feild et al., 1998). With exposure to progressively greater evaporative demand, the water loss rates of *Drimys* leaves with plugs compared to ones without plugs markedly diverged. Unplugged leaves exhibited a 70% decline in stomatal conductance with decreasing ambient relative humidity (from 105 to 35 mmol H₂O m⁻² s⁻¹ over 85% to 40% relative humidity drop). This degree of stomatal closure in response to dry air is similar to that reported for a wide variety of plants lacking stomatal occlusion. In contrast, stomatal conductances of plugged leaves decreased 10% over the same drop in relative humidity, from 100 to 90 mmol H₂O m⁻² s⁻¹ (Feild et al., 1998). The mechanism by which stomatal plugs prevent stomatal closure is unclear. It is possible that plugs may interfere with stomatal movements by maintaining a water vapor concentration around the guard cells that uncouples the guard cells from ambient conditions, or plugs may retard stomatal closure by physically interfering with guard cell movements (Feild et al., 1998). Regardless of the exact mechanism, these results provide physiological evidence that stomatal plugs in *Drimys* cannot be considered adaptations for drought.

In sharp contrast to their traditionally assigned role as anti-transpirants, the functional significance of stomatal plugs appears to be related to the occurrence of Winteraceae in areas that are generally wet (rainforests and cloud forests). One of the inevitable consequences of frequent rainfall and cloud cover is prolonged wetting of leaf surfaces (Brewer & Smith, 1997). Because CO₂ diffuses through water 10,000 times more slowly than in air, water films on leaf surfaces can create a high resistance to CO₂ diffusion into leaves for photosynthetic carbon gain. Photosynthetic measurements of *Drimys* leaves exposed to mist demonstrated that stomatal plugs allow relatively unperturbed photosynthetic activity when leaves are exposed to mist (Feild et al., 1998). Specifically, photosynthetic electron transport rates decreased approximately 40% following misting of *Drimys* leaves that lacked stomatal plugs. In contrast, electron transport rates of plugged leaves were unaffected by misting. Stomatal-associated waxes and cutin allow for continued gas exchange when leaves are wet because water droplets are repelled from the stomatal apparatus (Feild et al., 1998). These water-epidermis interactions keep the stomatal pore and intercellular spaces from being filled with water, which can occur when leaves are exposed to fog (Brewer & Smith, 1997). Further support for the efficacy of stomatal waxes in shedding excess water has been

observed in *Tasmania lanceolata*. Small trees of *T. lanceolata* that occur in eucalypt gallery forest understory and subcanopy, where they encounter frequent leaf wetting from canopy drip, have wax rodlets associated with their guard cells. In contrast, shrubby forms of this species growing on exposed ridge tops in alpine heathlands, which could presumably benefit from transpiration restriction, lack any epicuticular waxes associated with the stomatal apparatus (Feild, unpublished obs.).

These functional considerations provide a new perspective of the selective forces that may have driven the evolution of stomatal occlusion in Winteraceae. The observation that stomatal plugs, at least in *Drimys*, do not apparently protect leaves from drought is not consistent with the idea that these structures are adaptations that have played an important role in the persistence of a "primitive" vesselless phenotype. Further support for the new interpretation of stomatal plugs is that similar structures have evolved in other plants with vessels (such as some Myristicaceae and Epacridaceae; Koster & Baas, 1981), and without vessels (as in many rainforest conifers). All these plants occur in wet forest habitats. In addition, other vesselless angiosperms such as *Amborella*, *Tetracentron*, *Takhtajania*, and many conifers from drier habitats, lack stomatal plugs or other waxy structures obstructing the stomatal apparatus (Fig. 3A; Metcalfe, 1987; Brodribb & Hill, 1998).

VESSELLESS WOOD: HYDRAULIC LIMITATION OR ENHANCED FREEZING TOLERANCE?

Perhaps the best-known feature of Winteraceae is the lack of water-conducting xylem vessels in their wood (Bailey & Thompson, 1918; Cronquist, 1981; Gifford & Foster, 1989). Instead, the water-conducting system of Winteraceae is composed entirely of tracheids. Vessels are also absent in a number of other angiosperm groups such as *Amborella* (1 species), *Tetracentron* (1 species), and *Trochodendron* (1 species). Tracheids are xylem cells that lack cytoplasm such that their lumen provides an unimpeded path for water flow. Water movement between tracheids, however, requires that water must traverse cell walls (Zimmermann, 1983). The primary path for water movement between tracheids are pit depressions in the secondary wall, which although porous in construction, provide some resistance to flow (Zimmermann, 1983). In contrast, xylem vessels are water-conducting tubes generally larger than tracheids both in length and diameter (Carlquist, 1975; Zimmermann, 1983). Vessels consist of files of cells, with

each termed a vessel element, that unlike tracheids have substantially modified axial walls or perforation plates that allow for a more open pathway of water movement (Bailey, 1944; Carlquist, 1975; Zimmermann, 1983; Gifford & Foster, 1989). Vessel elements were apparently derived by a modification of the developmental program giving rise to tracheids, such that the pit membranes were hydrolyzed between the end walls of adjacent cells (Gifford & Foster, 1989). Vesselless wood has traditionally been considered a retained ancestral feature in angiosperms (van Tieghem, 1900; Bailey & Thompson, 1918; Bailey, 1944, 1953; Carlquist, 1975, 1983; Cronquist, 1981). What has propelled this idea is the assumption that vessels represent such an adaptive advantage that their subsequent loss is highly improbable (Carlquist, 1975). With the evolution of xylem vessels, botanists have argued that the early angiosperms were able to exploit habitats with uncertain water supplies and develop growth-enhancing traits such as large, undissected leaves and greater gas exchange rates (Carlquist, 1975; Doyle & Donoghue, 1986; Bond, 1989). By this perspective, hydraulically compromised plants such as Winteraceae have escaped extinction only by being restricted to wet cloud forest habitats (Carlquist, 1975, 1983, 1987).

The view that Winteraceae are primitively vesselless has been challenged by phylogenetic analyses (Young, 1981; Donoghue & Doyle, 1989; Chase et al., 1993; Mathews & Donoghue, 1999). Cladistic analyses indicate that the first angiosperms had vessels (albeit primitive ones), which were subsequently lost in several early angiosperm lines (Young, 1981; Donoghue, 1989; Donoghue & Doyle, 1989; Doyle, 1998). Although molecular phylogenies imply that *Amborella* and Nymphaeales are likely to be basal angiosperm branches and thus primitively vesselless (Mathews & Donoghue, 1999), both Winteraceae and Trochodendrales are nested within clades containing plants with vessels. Winteraceae are most closely related to Canellaceae, and Trochodendrales are included within eudicots (Chase et al., 1993; Soltis et al., 1997). To assume irreversible vessel evolution requires more evolutionary steps by additional independent origins of vessels in angiosperms (Young, 1981; Donoghue & Doyle, 1989). While the parsimony debt incurred by assuming that vessels cannot be lost was not overwhelming, this conclusion implies that the functional arguments for such an assumption should be examined (Donoghue & Doyle, 1989; Mathews & Donoghue, 1999). The cladistic arguments supporting vessel loss in Winteraceae have received much skepticism, primarily on the

grounds that no viable mechanism could drive the evolutionary loss of vessels, other than a shift to aquatic environments, as this would entail a shift to an inefficient hydraulic system (Carlquist, 1983, 1996). However, claims about the likelihood of vessel loss in Winteraceae need to be evaluated in a physiological context.

In support of this view, Donoghue and Doyle (1989) argued that little support exists for the view that vessel loss in Winteraceae is likely to have been selected against. First, the forests with low evaporative demand where most Winteraceae currently occur were suggested to be the type of habitats where any decrease in xylem transport capacity by vessel loss would have a relatively small effect (Donoghue, 1989; Donoghue & Doyle, 1989). Donoghue (1989) also suggested that the first vessels, hypothetically present in an ancestor of Winteraceae, were presumably of a primitive morphology containing numerous scalariform partitions, limited in number, and in a background of functional tracheids (Donoghue, 1989; Donoghue & Doyle, 1989). At this stage of low evolutionary specialization, the loss of vessels may not have been difficult, entailing only the retention of pit membranes. For example, the structural distinction and therefore the potential hydraulic consequences of having only tracheids versus having both tracheids and vessels is less obvious when Winteraceae are compared with their closest extant relatives, Canellaceae. Most Canellaceae vessel elements are similar in size and overall shape to tracheids of Winteraceae (Wilson, 1960). Tracheid diameters (16–69 μm ; Patel, 1974; Meylan & Butterfield, 1982; Carlquist, 1981, 1982, 1983, 1988, 1989) of Winteraceae overlap with the lower range of vessel element diameters reported from Canellaceae (20–140 μm ; Wilson, 1960; Metcalfe, 1987). Xylem conduits in Winteraceae and Canellaceae differ in that the pit membranes are retained in tracheids of Winteraceae, while in vessel elements of Canellaceae scalariform perforation plates are developed. Some Winteraceae species show an intermediate condition where the tracheid pit membranes are partially dissolved, forming relatively large porosities (0.05 μm diam.) as in some species of *Bubbia* (Carlquist, 1983). However, the comparative hydraulic properties of Canellaceae and Winteraceae xylem are not known.

Although it is difficult to determine the importance of specific selective pressures in the past, functional and physiological studies can indicate what factors might have been involved. Combined with information from historical biogeography, functional analyses also provide a context toward inter-

preting phylogenetic inferences about the past ecological and climatic associations of a lineage (Doyle et al., 1990). One common characteristic of the current distribution, ecological abundance, and paleomigratory patterns of Winteraceae is an association with cool, wet temperate environments. Paleoclimatological evidence suggests that at the time Winteraceae moved into Australasia, these southern high-latitude regions may have been colder than previously suspected, perhaps including some regions with persistent snow cover and frozen ground (Rich et al., 1988; Ditchfield et al., 1994; Sellwood et al., 1994; Stoll & Shrag, 1996). Where freezing temperatures are common, tracheids appear advantageous over vessels in terms of their resistance to freezing-induced cavitation (Hammel, 1967; Sucoff, 1969; Sperry & Sullivan, 1992; Sperry et al., 1994; Tyree et al., 1994; Davis et al., 1999). When stems freeze, the insolubility of dissolved gases in ice results in air bubbles. Upon thawing, these bubbles act as nucleation sites for the formation of air-embolisms blocking the movement of water through stems (Hammel, 1967; Sperry & Sullivan, 1992; Hacke & Sauter, 1996; Davis et al., 1999). The probability of a freeze-thaw event resulting in xylem embolism correlates with conduit volume (Sperry & Sullivan, 1992; Sperry, 1995; Davis et al., 1999). This is because a greater conduit volume results in both more numerous and larger air bubbles, which can easily expand to fill the entire xylem conduit during the thaw of xylem sap.

Most conifers are resistant to freeze-thaw-induced cavitation irrespective of the number of freezing events experienced because of their tracheid-based vascular system (Hammel, 1967; Sucoff, 1969; Robson et al., 1988; Sperry & Sullivan, 1992; Sperry et al., 1994). In tracheids, the bubbles produced in frozen sap are sufficiently small that they are collapsed by surface tension during thawing. In contrast, many vesselled angiosperms, and especially those with large conduit volumes, embolize extensively following one or more freeze-thaw events (Sperry, 1995; Pockman & Sperry, 1997; Davis et al., 1999). The tradeoff between vulnerability to freezing-induced cavitation and conduit size may have influenced the direction of xylem evolution in Winteraceae (Donoghue & Doyle, 1989; Donoghue, 1989). Indeed, Winteraceae have been documented to be relatively more frost tolerant compared to co-occurring plants with vessels. Sakai et al. (1981) demonstrated that the freezing resistance of buds, leaves, and stems of *Tasmannia lanceolata* was greater than most co-occurring angiosperms that had vessels (e.g., *Nothofagus*, *Eucalyptus*, and several Proteaceae) and was similar

to that of co-occurring conifers such as *Diselma*, *Microcachrys*, and *Phyllocladus*. *Drimys winteri* in southern Chile is also reported to be more tolerant to frost than *Nothofagus* species growing in the same environment (Alberdi et al., 1985). One part of the observed tolerance of Winteraceae to freezing may be the ability of a tracheid-based xylem to avoid freezing-induced limitations on stem water transport.

Despite the central position of xylem structure in discussions on the evolution of Winteraceae, no published reports exist for the hydraulic performance in the field. Clearly, comparative studies of xylem properties and water flux rates under field conditions are needed. However, the selective forces on wood evolution are not confined to hydraulic efficiency. Safety, with respect to avoidance of air embolisms, and mechanical strength are two additional selective pressures on the direction and pattern of xylem evolution in plants (Tyree et al., 1994). Certainly smaller xylem conduits offer higher resistance to water flow. Nonetheless, in colder climates tracheids appear to increase the overall hydraulic capacity by minimizing embolisms by freeze-thaw events (Sperry et al., 1994; Davis et al., 1999). This advantage for small-diameter xylem conduits for evergreen woody plants subject to freezing temperatures may explain the loss of vessels and a return to a tracheid-based vascular system in Winteraceae as indicated by phylogenetic analyses.

CONCLUSIONS

Studies of ecology, historical biogeography, and physiology challenge the long-held belief that Winteraceae are an unchanged and relictual angiosperm lineage. Further investigations into the structure and function of Winteraceae morphological features with respect to their natural environments will continue to inform discussions on their evolutionary history.

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